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BREEDING BIOLOGY AND BEHAVIOR OF HAMMOND'S AND WESTERN FLYCATCHERS IN NORTHWESTERN CALIFORNIA

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The Hammond's (*Empidonax hammondii*) and Western (*E. difficilis*) flycatchers are sympatric within portions of their breeding ranges in northwestern California. Westerns are common in a variety of habitats (Bent 1942:247, Johnson 1980:11-23); Hammond's are more abundant at higher elevations (Bent 1942:226, Johnson 1963:140-143). Only one major study of each species' breeding biology has been reported; both looked at the species in places where they do not occur together. Davis et al. (1963) studied the breeding biology of Westerns in a hardwood-dominated forest in northern Monterey County, California. Davis (1954) studied the breeding biology of Hammond's in mixed coniferous and deciduous forests at Flathead Lake, Montana. More knowledge is needed of both species' breeding ecology and behavior where they are sympatric on their nesting grounds. I report here on a comparative study of the breeding behavior and biology of color-marked birds.

STUDY AREAS AND METHODS

I selected twelve stands of Douglas-fir (*Pseudotsuga menziesii*)-hardwood forest in Humboldt and Trinity counties of northwestern California (Figure 1). The 12- to 20-ha stands were selected on the basis of size and accessibility. They lie between 710 and 1235 m elevation. Between April and August, four observers spent 1444 total person-hours in the field in 1984; two observers spent 2442 total hours in 1985 and 836 total hours in 1987. On the basis of my observations of both species' phenology, I divided observations into four periods: prenesting (10 April to 15 May), nest building and incubation (16 May to 15 June), brooding (16 June to 15 July), and postbrooding (16 July to 15 August). Despite some differences in nesting phenology, I believe that the two species' nesting behaviors were sufficiently synchronous that this classification is satisfactory for both.

Three Western and two Hammond's nests were intensively observed from the nest-building phase through the fledging of the young. Additional information came from observation of 2 to 21 additional Hammond's nests and 13 to 81 additional Western nests. Incubation periods were determined from the laying of the last egg to hatching of the young. For both species, I used the first day the female was sitting in the nest as the day of laying of the last egg, and the day when the young were first fed as the day of hatching of the last young.

I estimated nest success by using Mayfield's model (1961, 1975), in which nest observations are treated as discrete units for computation of specific development stages (e.g., incubation or nestling). Mayfield's model is based on the concept of exposure days: one nest observed for 1 day equals 1 exposure day. This model incorporates all observed nests, both successful and unsuccessful, and accounts for the length of time each was observed.

Mist nets were placed near foraging pairs and near routes to and from nests. Birds were sexed as males if they had a cloacal protuberance (Salt 1954, Wolfson 1954) or as females if they had a brood patch (Bailey 1952, Hinde 1962), and they were aged by skull pneumatization (Norris 1961). In addition, Westerns with incompletely pneumatized skulls were aged according to the plumage criteria of Johnson (1974). Hammond's with incompletely pneumatized skulls were also aged according to the shape of their rectrix tips (Johnson 1963).

In the analysis of the data, all years and all stands were combined. I used a contingency table (Sokal and Rohlf 1981) to test the null hypothesis of no difference between the ages (older than two years versus younger or second

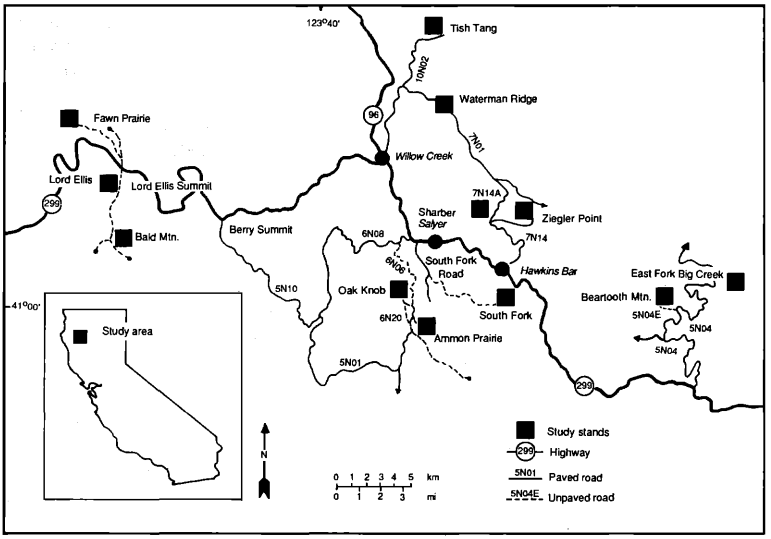

Figure 1. Locations of the study areas in northwestern California.

year) of breeding adult Westerns. The samples for Hammond's consisted of fewer than 5 observations per cell so I did not conduct the test for that species.

RESULTS

Nesting Chronology

Hammond's Flycatchers were found as summer residents in 6 of the 12 study stands, with the earliest birds arriving on 24 April (Figure 2). Their numbers increased up to around mid-May. Westerns were summer residents in all study areas, with the earliest birds arriving on 7 April (Figure 2); their numbers increased until around 20 April. Although Hammond's arrived on the breeding grounds later than Westerns, they fledged young at about the same time (Figure 2).

Sex Identification by Aural Cues

I noted that the Westerns had two notes, a metallic "pink" and a more hollow "pik." The "pik" note was given by both sexes and was usually heard during the nestling period, whenever adults brought food. Incubating females gave the "pink" note before they left the nest and, while off the nest, consistently gave a series of these calls, probably serving as location or alarm notes. The male Westerns occasionally gave a similar alarm call, whenever Steller's Jays (*Cyanocitta stelleri*) were close to the nest. The female rarely called from the nest except to emit a few "pink" notes just before departing, probably in response to the calling male. While off the nest, she repeatedly gave "pink" alarm or location calls, while the male responded with "tsuuit"

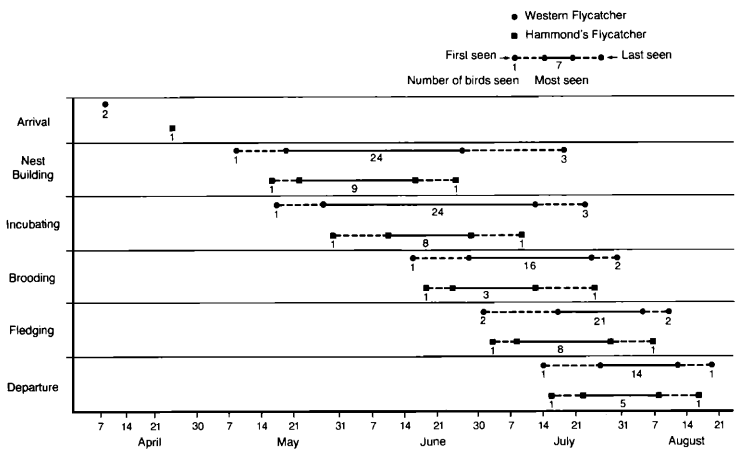

Figure 2. Nesting chronology of Hammond's and Western flycatchers on breeding grounds in northwestern California, as determined from behavioral observations and censuses conducted in 1984, 1985, and 1987.

position calls. When jays were nearby, the male frequently sounded the "seet" alarm call, while the incubating female sat quietly in the nest. In four cases, however, the male also used the "pink" alarm call when jays were close to the nest. Males also gave "tsuuit" position calls prior to the female's leaving the nest. A harsh "chrrip" was given by males engaged in chasing encounters.

Both sexes of Hammond's emitted a harsh "peep" call, which they used as an alarm note while engaged in chasing bouts. The females also gave occasional crisp "pip" location calls while off the nest. Females always left the nest and returned to it silently.

Skull Pneumatization and Age of Breeding Adults

Birds older than two years (after second year, ASY) were distinguished from second-year (SY) birds on the bases of skull pneumatization and rectrix shape. ASY Westerns were found in higher proportion in June than in July ($\chi^2 = 18.42$, df = 1, $P < 0.001$) (Figure 3). ASY Hammond's were also found in higher proportion in June than in July; however, the sample size was small.

The Nest

Hammond's nests appeared distinctly different from Western nests. The outer bowl of 21 Hammond's nests were taller, more tightly woven, and mimicked the surrounding substrate more than did 81 Western nests. The outer bowl of the single retrieved Hammond's nest contained mostly white scale lichens (e.g., *Hypogymnia inactiva),* moss (e.g., *Dendroalsia abietina, Homalothecium nutallii*), bryophytes (e.g., *Porella navicularis, Isothesium* sp., and *Alsia* sp.), and some stringy lichen (*Ramalina menziesii*). Stringy lichen, bird feathers, and Douglas-fir leaf scales lined the cup. In fourteen observations, a hovering female Hammond's gathered scales up to six consecutive times from the outer foliage of Douglas-fir branches.

The outer bowl of 22 retrieved Western nests contained mostly moss and some scaly lichen (*H. inactiva*), occasionally the paper-thin bark of the madrone (*Arbutus menziesii*) and other coarse materials. Stringy lichen lined the cup. These nests were not camouflaged because the same types of nesting materials were used on all substrates. Even nests built on grassy banks did not include grass in the bowl construction but resembled the typical moss-lichen nest. The moss and lichens were held together with spider webs, which also helped secure the nest base to a surface.

Nest Building

In 14 hours of observation of three color-marked pairs of Hammond's Flycatchers, a male was observed assisting the female in gathering Douglas-fir scales for the nest lining only twice. While building the nest, the female compressed the material by rotating herself in the nest. Observations at two nests suggested that both pairs took about 5 to 6 days to complete their nests. Among all four color-marked pairs of the Western observed over the complete building sequence, only the female was seen building the nest. Nest completion averaged 5.5 days (range 5-6 days; SD = ± 0.58; $n = 4$).

Both species renested following nest predation or abandonment. Sixteen pairs of Westerns and seven pairs of Hammond's were observed building second nests, and two pairs of Hammond's nested three times. However, the species differed markedly in their methods of building replacement nests. In all instances of nest abandonment, Hammond's females completely removed all material from the old nest to use in building the replacement. In contrast, female Westerns did not remove any material from abandoned nests for renest attempts. It was not unusual to find replacement nests of both species close to their abandoned nests. In 1984, a female Hammond's built a second

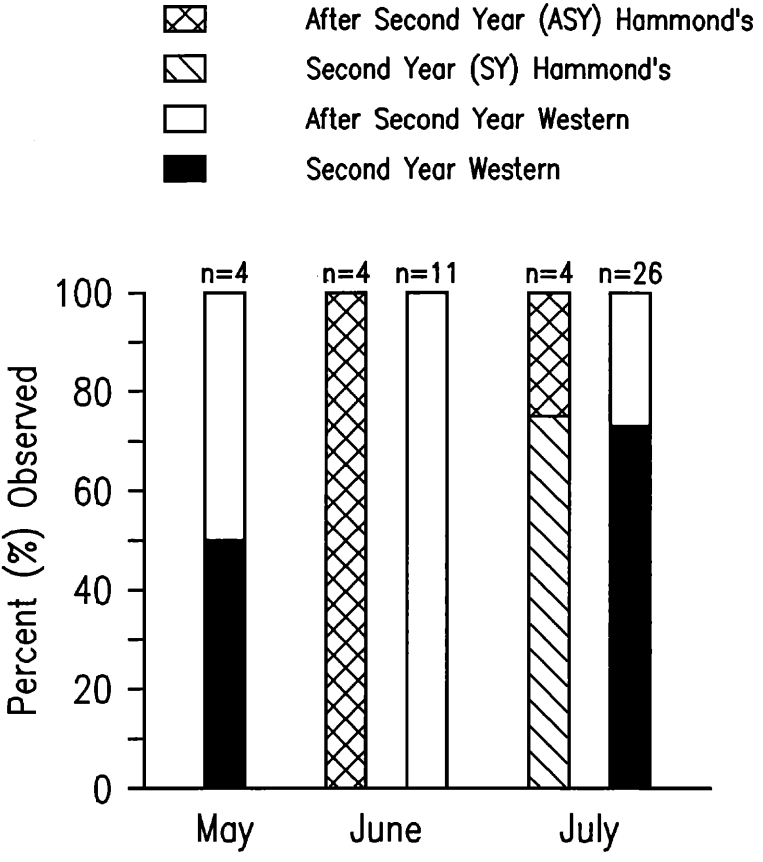

Figure 3. Chronological changes in age composition of mist-netted Hammond's (n = 8) and Western Flycatchers (n = 41) in Humboldt and Trinity counties, as determined by skull pneumatization and rectrix shape. Ages: after second year = adult birds with 100% ossification and blunt rectrix tips; second year = subadult birds with 90% ossification and pointed rectrix tips.

nest in the same tree as the first, and a third nest was built 10 m from the second. In 1985, a pair built a second nest about 20 m from the first and a third about 11 m from the second. In 1985 and 1987, female Westerns built second nests an average of 15 m (range 4-46 m; SD = ± 10.2; n = 13) from their abandoned nests.

Clutch Size

A single Hammond's nest, observed in 1985 during late incubation, had three eggs. Observations of two other Hammond's nests in early incubation suggested that the female took 4 days to lay a clutch of at least three eggs, since three nestlings fledged. The average clutch size for Western was 3.3 eggs (range 2-4 eggs, SD = ±0.52, n = 33) per nest.

Incubation and Nest Attentiveness

In both species, only the female incubated. On the basis of two intensively studied successful nests, Hammond's spent 15.5 days incubating. Female Westerns in three intensively studied successful nests spent an average of 16 days (range 15-17 days; SD = ± 1.0) incubating.

The two species were alike in nest attentiveness (Figure 4). In both species, the incubating female foraged for herself, the male rarely visiting. I found that the male Westerns remained within 25 m of the nest tree. However, they remained quiet unless predators, such as jays, were nearby.

It was easier to predict for the Western than for the Hammond's when a female was planning to return to its nest. Western females frequently gave a "pink" note while off the nest, but before returning they suddenly became silent. The female rarely flew directly to her nest. Instead, she would fly close to the nest and quietly sit on a perch, flicking her tail for several seconds to a minute, before flying to the nest. Hammond's females were usually rather quiet while off the nest. They generally flew silently and directly to the nest without pausing on any perch.

Parental Care of the Young

I observed no male Western Flycatchers brooding; however, I once observed a male Hammond's Flycatcher already brooding when observations began at 0900. He continued to brood for 7 min before being relieved by the female. At the three regularly observed Western nests, nestlings were brooded solely by the female for an average of 5.3 days (range 5-6 days; SD = ±0.53). Western females at three intensively studied nests spent close to 90% of their time brooding in the early part of this period (Figure 5). Observations of two intensively studied nests revealed that Hammond's covered their young for periods of 5 and 6 days.

In two regularly studied Hammond's nests, the nestling period took 16 days for one nest and 17 for the other. Over 29 hours of observation, both male and female Hammond's fed the nestlings from the first day of hatching. For Westerns, the nestling period took 16 days for two nests and 17 days for one. On the basis of 71 hours of observing three nests, I found that both male and female Westerns fed the nestlings.

The feeding rate for two pairs of Hammond's increased after the first two days, leveled off after a week, and remained there before declining sharply prior to fledging (Figure 6). The feeding rate at three Western nests had two peaks, on the 6th and 11th days (Figure 6).

Fledging Period

Young of both species displayed similar fledging behavior. In two Hammond's nests, the nestlings started to move actively about in the nest about a

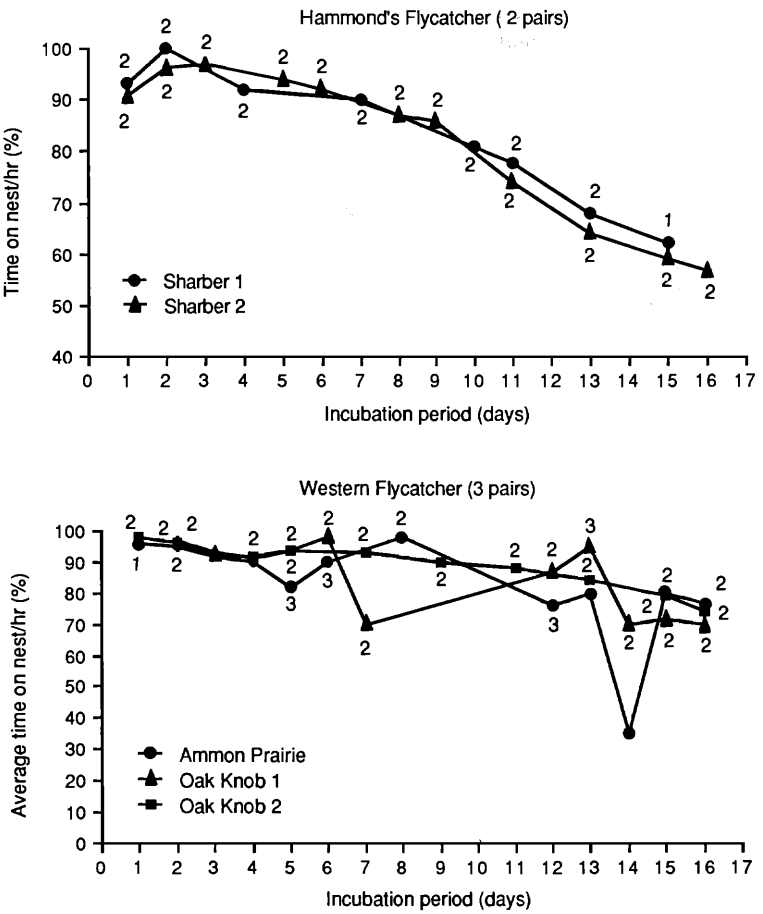

Figure 4. Nest attentiveness of incubating female Hammond's and Western flycatchers, as determined from successful nests. Numbers accompanying each point indicate the number of continuous hours of nest observation on which the percentage is based.

week before fledging. Five days before fledging, they exercised their wings. At two days before fledging, the fully feathered nestlings flapped vigorously from the nest rim and then flew intermittently to nearby twigs. Although the actual departure from the nest was not observed, the young remained in the stand for at least a week, when the young were seen with the banded adults approximately 175 m from the nest tree.

Western young actively flapped their wings 3 to 4 days before vacating the nest. For nests built on ledges of natural cavities, no practice flights were observed, although the young fluttered while perched on the cavity rim. The young were very uncoordinated during fluttering. They remained within 0.5 m of each other while perched quietly in trees near the nest tree. Fledged young chirped loudly and quivered their wings whenever adults brought

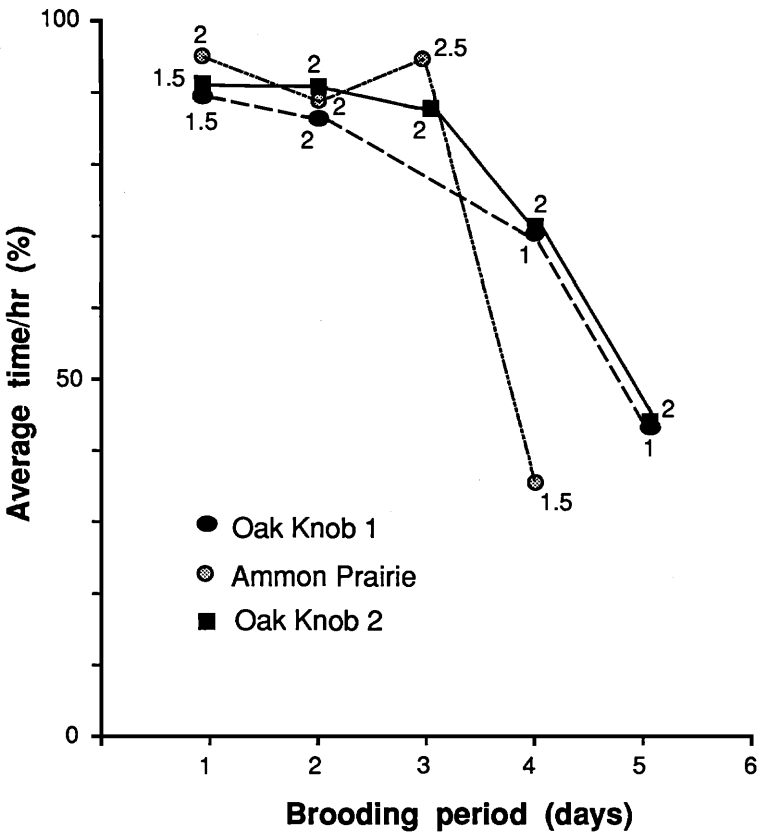

Figure 5. Nest attentiveness of three pairs of brooding female Western Flycatchers. Numbers accompanying each point indicate the number of continuous hours of nest observation on which the percentage is based.

food. Following fledging, the young did not return to the nest tree but stayed near the nest stand for at least 6 to 7 days.

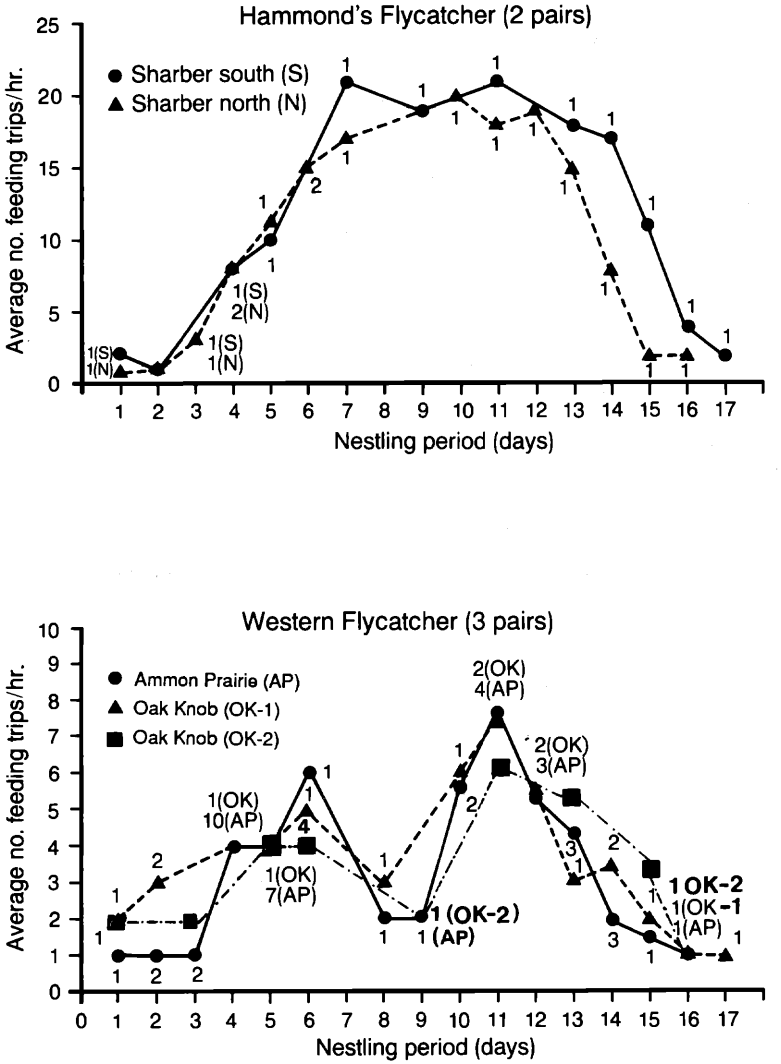

Figure 6. Feeding rates over the nestling period of Hammond's and Western flycatchers at successful nests. Numbers accompanying each point indicate the number of continuous hours of nest observation on which the average number of feeding trips per hour is based.

Site Tenacity

Site tenacity was documented in three instances. A banded female Western built her first nest about 30 m from the previous year's site but subsequently abandoned it when the third egg was damaged. She relocated to the previous year's site, atop the old nest, and fledged a brood. The other color-banded birds, a female Western and a male Hammond's, were observed breeding in the vicinity of the nest site of the previous summer. All three color-marked birds were paired with new unbanded mates.

Nesting Success

For Hammond Flycatchers, the estimated survival probability was 49% during the incubation period and 51% during the nestling period (Table 1). The probability of survival through both periods was 48%. The number of total exposure days during the incubation and fledging periods was 32.0. For Western Flycatchers, the estimated survival probability was 46% during the incubation period and 55% during the nestling period (Table 1). The total exposure days for both periods were virtually the same as for Hammond's.

For Westerns, nest-site selection accounted for 21% (6 of 29 nests observed during nest building) of the total nest failures. Of the six failed nests placed between loose bark, four were built by yearling females. For Hammond's, one out of ten known failures observed during the nest-building period was due to nest-site selection. This nest was built on branches exposed to strong prevailing winds and was destroyed during a windstorm.

Nest predation during the incubation and nestling periods also contributed to nest failure of both species. Of ten Hammond's nests studied during the periods of incubating and brooding, predators took five. Three of them were preyed upon by Steller's Jays. Of 41 nests of incubating and brooding Western Flycatchers, 14 with eggs or nestlings were victimized by predators. I observed Steller's Jays prey on 10 of these nests and a Chickaree (*Tamiasciurus douglasi*) take one nest with eggs. The other two nests lost to

Table 1 Survival Probabilities of Hammond's and Western Flycatchers

Species and Study	Nests	Nests lost	Nest days	Daily survival probability	Exposure days	Survival probability
Incubation period						
Western						
This study	37	23	490	0.95	16.0	0.46
Davis et al. (1963)	23	2	304	0.99	15.0	0.86
Hammond's	12	5	112	0.96	15.5	0.49
Brooding period						
Western						
This study	34	18	506	0.96	16.5	0.55
Davis et al. (1963)	20	4	220	0.98	16.0	0.75
Hammond's	7	2	50	0.96	16.5	0.51

predation I also suspected to have been plundered by Steller's Jays. The lining of these two nests resembled the pulled lining of the five nests taken by jays. These pulled linings were caused by the resisting chicks grasping the lining as the jay pulled them from the nest.

DISCUSSION

I found the following differences and similarities between the breeding biologies of Hammond's and Western flycatchers: (1) incubating female Westerns were more predictable in returning to nests than Hammond's; (2) Westerns did not reuse materials from abandoned nests as did Hammond's; (3) Westerns arrived on the breeding grounds much earlier than did Hammond's, yet both fledged young at about the same time; (4) the outer bowls of Hammond's nests were higher and more tightly woven than those of Western nests; (5) site tenacity was observed for both species, when they relocated at nest sites used the previous summer; and (6) selection of poor nest sites and predation of nests by Steller's Jays and Chickarees contributed to the poor nesting success in my study area. Observations of color-marked Hammond's and Western also helped to corroborate some observations made by Davis (1954) and Davis et al. (1963). However, I found the following differences between my results and those of Davis et al.: in my study area (1) male Westerns did not call frequently to incubating females; (2) the birds did not produce second broods if the first brood fledged; (3) survival rates were much lower during incubation and brooding periods; (4) females remained quiet during the incubation and brooding periods; and (5) males sometimes sounded like females, as they occasionally uttered the "pink" note. These apparent differences between studies illustrate the importance and need for more descriptive studies of nesting behavior throughout a species' range.

The finding that Westerns did not lay second clutches was supported by the fact that young did not appear until the first week of July. The young birds are easy to detect after fledging because of their vociferous behavior and their parents' highly visible and frequent feeding trips. Both species migrate from the study sites between late July and early August, leaving no time to renest.

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